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Abstract

Stimuli briefly flashed just before a saccade are perceived closer to the saccade target, a phenomenon known as saccadic compression of space. We have recently demonstrated that similar mislocalizations of flashed stimuli can be observed in the absence of saccades: Brief probes were attracted towards a visual reference when followed by a mask. To examine the spatial profile of this new phenomenon of masked-induced compression, here we used a pair of references that draw the probe into the gap between them. Strong compression was found when we masked the probe and presented it following a reference pair, whereas little or no compression occurred for the probe without the reference pair or without the mask. When the two references were arranged vertically, horizontal mislocalizations prevailed. That is, probes presented to the left or right of the vertically arranged references were "drawn in" to be seen aligned with the references. In contrast, when we arranged the two references horizontally, we found vertical compression for stimuli presented above or below the references. Finally, when participants were to indicate the perceived probe location by making an eye movement towards it, saccade landing positions were compressed in a similar fashion as perceptual judgments, confirming the robustness of mask-induced compression. Our findings challenge pure oculomotor accounts of saccadic compression of space that assume a vital role for saccade-specific signals such as corollary discharge or the updating of eye position. Instead, we suggest that saccade- and mask-induced compression both reflect how the visual system deals with disruptions.

Keywords

Compression of space, masking, perceptual mislocalizations

1. Introduction

Localizing objects, that is, registering *where* objects are in our environment is a fundamental task of the visual system.However, when probe stimuli are only briefly flashed, previous research has described systematic biases when observers are asked to localize the probe. Some of the most remarkable mislocalization effects have been reported around the time of saccadic eye movements.In complete darkness,stimuli flashed briefly before or in the early phase of a saccade are strongly mislocalized in the direction of the eye movement, independently of where in the visual field the probe is flashed(Honda, 1989, 1991; Matin, Matin, & Pearce, 1969; Matin, Matin, & Pola, 1970). In contrast, under conditions of dim illumination (e.g. in a dimly-lit room or with stimuli presented on a computer screen with a slightly illuminated background), the pattern of mislocalizations changes: flashed probes are perceived closer to the target of the saccadic eye movement(Honda, 1993, 1999; Lappe, Awater, & Krekelberg, 2000; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). That is, flashes presented between the fixation point and the saccade target are mislocalized in saccade direction, whereas flashes presented beyond the saccade target are mislocalized against saccade direction. Due to theconvergence of localization responseson the location of the saccade target, the phenomenon has become known as saccadic compression of space(Ross et al., 1997).

As these mislocalization effects were discovered in the context of saccades, most authors have attributedtheir originto saccade-specific phenomena. Specifically,the mislocalizations are assumed to be capturing intermediate stages in the transformation from pre- to post-saccadic coordinates under the direction of extraretinal signals related to the eye movement, for instance eye position signals, saccade vector information or corollary discharge (Dassonville, Schlag, & Schlag-Rey, 1992; Hamker, Zirnsak, Calow, & Lappe, 2008; Honda, 1993; Matin et al., 1970; Morrone et al., 1997; Richard, Churan, Guitton, & Pack, 2009; Teichert, Klingenhoefer, Wachtler, & Bremmer, 2010; VanRullen, 2004; Ziesche & Hamker, 2011). These coordinate shifts have been well documented in theproperty changes of receptive fields of visual neurons around the time of saccades(Duhamel, Colby, & Goldberg, 1992; but see Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). In general, these coordinate shiftsensure that we perceive the visual world around us as stable, in spite of drastically changing retinal input with every eye movement(see Bays & Husain, 2007; Cavanagh, Hunt, Afraz, & Rolfs, 2010; Melcher, 2011; Sommer & Wurtz, 2008 for recent overviews).

However, otherfindings have challenged the claim that the observed mislocalizations are exclusively related to and caused by eye movements. For instance, when the visual consequences of saccades are simulated by moving the stimuli and their background at saccadic speed while participants remain fixated, mislocalizations similar to those observed with real saccades can be observed(Honda, 1995; MacKay, 1970; Morrone et al., 1997; O'Regan, 1984; Ostendorf, Fischer, Gaymard, & Ploner, 2006). Although qualitatively similar, there are often differences in magnitude or in the time course of effects when comparing real saccades to "simulated" saccades, leaving the possibility that there is still an aspect that is inherently saccadic to the specific pattern of mislocalizations. In particular, saccadic compression of space,including a strong mislocalization component against saccade direction for stimuli presented beyond the saccade target,has been elusive when simulating saccades with image motion(Morrone et al., 1997; but see Ostendorf et al., 2006).

Recently, we have reported a mask-induced compression effect in the perceived locations of briefly flashed probes in a condition with neither image motion, nor saccadic eye movements(Zimmermann, Born, Fink, & Cavanagh, 2014; Zimmermann, Fink, & Cavanagh, 2013). Participants held fixation throughout a trial while first a visual reference stimulus was presented in the periphery, followed by a flashed probe and a whole-field random texture mask. Participants had to localize the probe and the reference was irrelevant to the task. Nevertheless, participants' localization responses were biased towards the reference stimulus, even though they remained as precise (i.e. similar variance in the localization responses) as in the unmasked control.Indicative of compression, the biaswas found both for probes more foveal and for probespresented more peripheral than the reference: all appeared shifted toward the reference. Furthermore, strong compression was only observed when the mask was presented close in time to the probe, and when the reference stimulus' onset occurred in a time window 70-200 ms before the probe and mask.

These results shed an entirely new light on compression effects andpoint tocontributions from mechanisms unrelated to saccades and retinal image motion. To better understand these mechanisms, the current experiments examine the two-dimensional profileof mask-induced compression induced with different reference stimulus configurations and test its robustness by comparing two response modes: mouse clicks to indicate remembered probe location, or saccades to the probe location. The basic procedure was similar to that used in our previous work (Zimmermann, Born, et al., 2014; Zimmermann et al., 2013): we presented a salient visual reference stimulusfollowed by a mask to induce compression in

the perceived space of briefly flashed probes.In contrast to the previous studies, results were compared to a condition withreferences and no mask and a condition with a mask but no references. Compression in perceived probe locations was only found with both, references and mask. Further, we used two reference stimuli that were spatially separated either vertically(Experiment 1) or horizontally(Experiment 2).We found in both arrangements that perceived probe locations were compressed towards the references and that compression was stronger orthogonally to the axis joining the two reference stimuli as opposed to along that axis. Finally, when we compared mislocalizations in perception to the misdirection of fast,voluntary movements towardsthe probe (i.e., saccades),the distribution of saccade endpoints was compressedtowards the references in the same way asthe perceptual judgments, indicating that the saccade system is subject to the perceptual illusion. Note that when we use a saccade as a method of reporting the probe location, the mislocalization is still induced by the mask, not the saccade.The saccade followsthe probe presentation by 270-280 ms (average saccade latency in the current experiments), as a measure of the mislocalization. At first glance, the introduction of the saccade confuses the attempt to evaluate mislocalization in the absence of saccades.But the saccade target in this technique was the probe itself.Thus, saccadic compression should not interact with the mask-induced compressiontowards the references, as saccadic compression is always toward the saccade target (the probe here) and, in any case, the delay between the probe and the saccade falls outside the range of delays where saccadic compression is seen (e.g., Ross et al., 1997) .

2. Experiments 1a and 1b: Vertically arranged pair of references

In the previous articles on mask-induced spatial compression (Zimmermann, Born, et al., 2014; Zimmermann et al., 2013), the perceived probe location was often shifted to the reference to the extent that it overlapped. This caused difficulty in differentiating between a shifted probe, seen flashed on top of the reference, and a probe that was just not seen at all.Thus, we cannot fully exclude that sometimes participants may have reported the reference location when they were unsure of what they had seen. Since our probes are set to be low contrast (or short duration), we needed to avoid any confusion between unseen probes and probes that are fully compressed, overlapping the reference stimulus. Our use of two reference stimuli in these new experiments addresses this issue as it allows a probe to be drawn into the gap between the two references.A trial with complete compression (all

three stimuli will be seen) can then be easily differentiated from a missed probe (only two will be seen). Having two references also let us explore the spatial profile of compression.

Methods

Participants

The two experiments were run on eight participants each (Experiment 1a: six women, two men, including one author, mean age: 32.9 years; Experiment 1b: three men, five women, including the same author and one further participant from Experiment 1a, mean age: 32.0 years). One participant in Experiment 1b reported strabismus and therefore completed the experiment under monocular viewing conditions, with one eye patched and stimuli presented in the nasal hemifield. The response pattern for this participant was comparable to the others and inclusion/exclusion did not change the results of the statistical analysis.All other participants reported normal or corrected-to-normal vision. For all experiments reported in this study, observers gave written informed consent prior to participating and the procedures followed the principles laid down in the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Apparatus

Subjects were seated 57 cm from a Compaq P1220 CRT monitor (Houston, TX, USA) with head stabilized by a chin- and headrest. The visible screen diagonal was 22 inches, resulting in a visual field of 40.2 x 30.5 deg. Stimuli were presented with a monitor refresh rate of 120 Hz at a resolution of 1024 x 768 pixels. The experiment was programmed in Matlab (The MathWorks Inc., Natick, MA, USA) using the Psychophysics and Eyelink Toolbox extensions (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002; Pelli, 1997). Eye movements were recorded using an EyeLink1000 desk-mounted eye tracker (SR-Research Ltd., Mississauga, ON, Canada) at a sampling rate of 1000 Hz.

Stimuli, design and procedure

The sequence of events is illustrated in Figure 1A. All stimuli were presented on a homogeneous, gray background. A trial started with the presentation of a black fixation square (0.5 deg side length) 6 deg to the left or right of the screen center (counterbalanced across participants), on the horizontal meridian. After 800 ms, two vertically arranged reference dots (radius: 0.5 deg; vertical distance from the horizontal meridian: ± 4 deg) were

presented at a horizontal distance of 12 deg from fixation (i.e. 6 deg from screen center, opposite to fixation). The references were either red or blue (color counterbalanced across participants), stayed on screen for 183 ms and were followed by a 50 ms blank interval. After the blank, the probe was briefly flashed (dot of likewise 0.5 deg radius; color likewise red or blue, but alwaysopposite to the reference color), followed by a 50 ms full screen pattern mask (gray squares of randomized luminance, 0.7 deg side length).

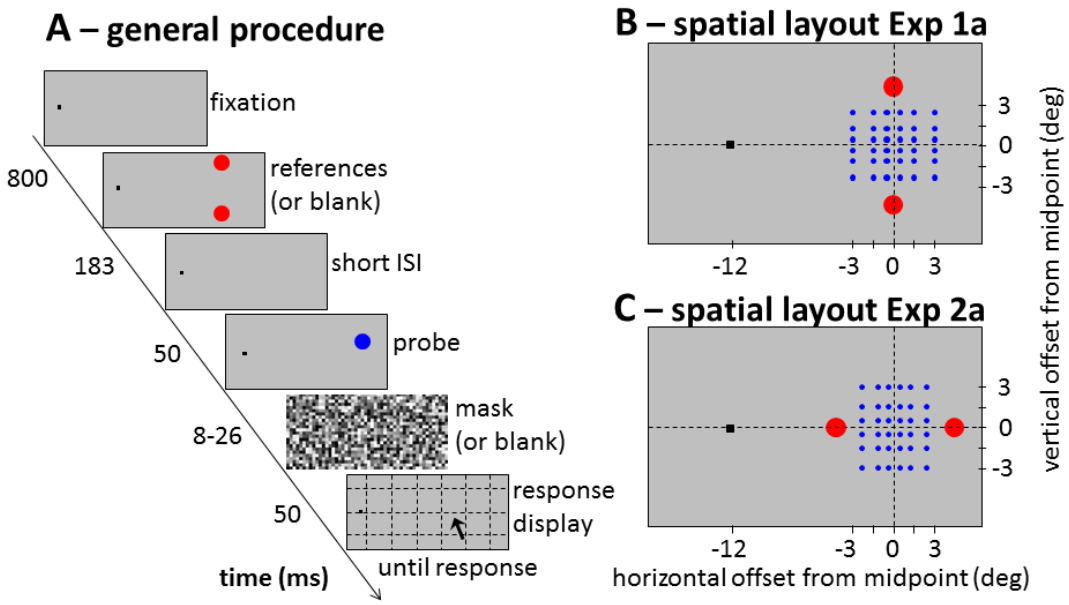

Figure 1.Experimental procedure for all experiments(*A*). Red dots represent the references, the blue dot the probe. Spatial layout for Experiment 1a (*B*) and Experiment 2a (*C*).Blue dots in *B* and *C* illustrate the tested probe locations with respect to the midpoint between the two references (illustrated by the intersection of the two dotted lines; these lines were only visible as part of the larger response grid shown during the response phase when stimuli were already off the screen). Spatial relations between stimuli are drawn to scale, but probes were as large as the references and only one probe was shown per trial. Negative values mean probes were presented more foveal/below the midpoint between the two references, positive values indicate probes were presented more peripheral/above the midpoint. Colors of references and probe as well as the hemifield in which the stimuli were presented were counterbalanced across participants. ISI = interstimulus interval

After the mask, the mouse cursor appeared.For each trial, the cursor was placed at a random position, maximum distance ± 4 deg horizontally, ± 6 deg vertically from the midpointbetween the two references.Additionally, we presented a reference grid consisting of horizontal and vertical dotted lines, covering the entire screen (lines 1.9 degapart, with one of the horizontal lines on the horizontal meridian, and one of the vertical lines on the reference axis, i.e., the imaginary line joining the two references). The rationale behind the response grid was that previous studies on saccadic compression have demonstrated larger compression effects when a ruler provided a visual reference after the saccade, that is, at

the time the localization response was given(Lappe et al., 2000). Following these observations, we presented the grid, a two-dimensional ruler, to increase our chances to get strong compression effects.

Experiment 1a: Participants were required to keep their gaze on thefixation square throughout the stimulus presentation (controlled by eyetracking) and to indicate at the end of a trial where they had perceived the probe with a mouse click. With onset of the response display, they were free to move their eyes. If they hadn't seen the probe, they were instructed to click on the fixation square. Probe duration was adjusted individually for each participant and block making use of these "not seen" responses: initial probe duration was set to 17 ms.With each click on the fixation square indicating an unseen probe, probe duration was increased by one refresh cycle (8.3 ms).Four localization responses in a row led again to a decrease of probe duration by one refresh cycle (i.e., staircase procedure following a 4-down, 1-up rule).The minimum probe duration was fixedat one refresh cycle. The probe's location was pseudo-randomly chosen on each trial from six possible horizontal, and six possible vertical offsets: it was presented at a distance of either -3, -1.5, -0.5, 0.5, 1.5, or 3 deg horizontally from the reference axis (negative values: closer to fixation than references, positive values: more peripheral than references) and -2.4, -1.2, -0.4, 0.4, 1.2, or 2.4 degvertically from the midpoint between the two references (i.e., the horizontal meridian; negative values: below, positive values: above).The 36 resulting probe locations and the scaling (with respect to the midpoint between references) are illustrated in Figure 1B. Each probe location was tested five times, resulting in a minimum of 180 trials per block. Trials in which participants clicked on fixation ("not seen") and trials in which the eyetracker detected a break of fixation (horizontal gaze coordinate more than 1.5 deg away from fixation at the time of mask onset) or a blink (for both: written feedback given on screen) were repeated at the end of a block. In addition to the experimental block (references+mask), each participant completed two control blocks (both same number of trials as the experimental block): The references-only block was identical to the experimental block except that no mask, but a 50 ms blank screen was presented after the probe. The mask-only block was identical to the experimental block except that no references, but a 183 ms blank screen was presented instead (extending the blankinterval before probe presentation to1033 ms). The response grid was present in all conditions after the mask/blank. The order of conditions (references-only, mask-only, references+mask) was counterbalanced across participants.

Experiment 1b: The procedure was identical to Experiment 1a with the exception that participants were required to saccade towards the perceived probe location as soon as they detected the probe. After the saccade, they additionally indicated the perceived location with a mouse click. Further, probes were always presented on the horizontal meridian (no vertical offsets), but their horizontal location on each trial was chosen from the same six possible offsets as used in Experiment 1a: -3, -1.5, -0.5, 0.5, 1.5, or 3 deg from the reference axis. Each probe location was tested at least 25 times, resulting in at least 150 trials per block. However, trials in which participants clicked on fixation ("not seen") and trials in which the eyetracker detected anticipatory saccades (latency < 100 ms), breaks of fixation (horizontal gaze coordinate more than 1.5 deg away from fixation at the time of probe onset), blinks, or no saccade within 600 ms after probe onset were repeated at the end of a block. As in Experiment 1a, participants completed one references+mask block, one references-only block and one mask-only block with order counterbalanced across participants.

Results and Discussion

Error trials and probe duration

Experiment 1a: Breaks of fixation or blinks were detected on 4.0% of trials. Participants reported not having seen the probe (click on fixation square) on 0.5% of trials in the references-only condition, 12.5% of trials in the mask-only condition, and 12.4% of trials in the references+mask condition. This suggests that the probe was easier to detect in the references-only condition, but of similar visibility in the mask-only and the references+mask condition. Due to the adjustment of probe duration based on those "not seen" responses, average probe duration was 10 ms in the references-onlycondition, and 18 ms in both conditions with the mask. Pairwise t-tests confirmed a significantly shorter duration in the references-only compared to the other two conditions, $ts(7) > 4.43$, $ps < .003$, but no difference between the mask-only condition, and the references+mask condition, $t(7) = 0.47$, $p = .653$.

Experiment 1b: The stricter criteria for trial exclusion based on the saccade characteristics led to overall more rejected trials (17.7%) compared to Experiment 1a. However, "not seen" responses occurred with similar frequency as in Experiment 1a: on 0.6% of trials in the references-only condition, on 11.0% of trials in the mask-only condition, and 10.0% of trials

in the references+mask condition. This resulted in average probe duration of9 ms in the references-onlycondition, and 21 ms in the mask-only, and 20 ms in the references+mask condition. Pairwise t-tests confirmed a significantly shorter duration in the references-only compared to the other two conditions, *t*s(7)> 4.41, *p*s< .003, but no difference between the mask-only condition, and the references+mask condition, *t*(7) = 1.25, *p* = .250.

Localization responses

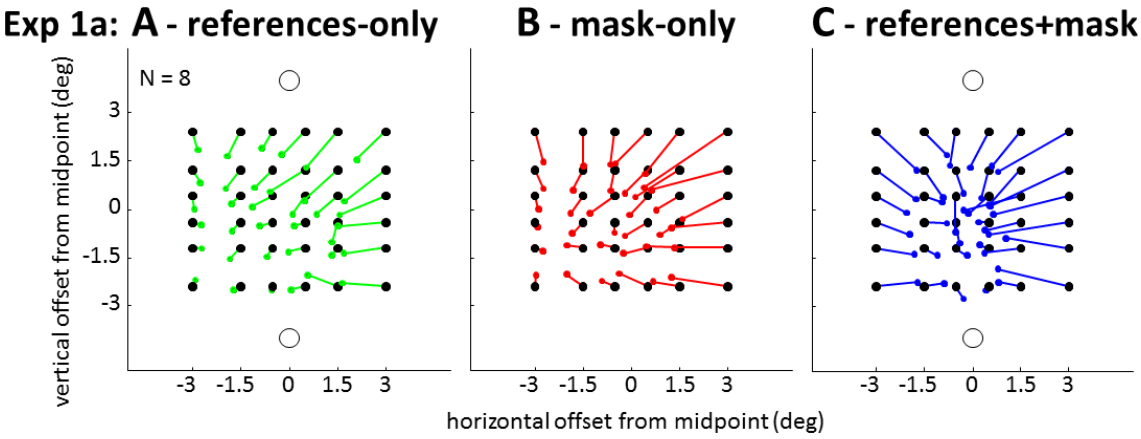

Figure 2. Actual (black dots) vs. perceived (colored dots) probe location for the 36 tested locations in the three conditions of Experiment 1a (responses averaged over all eight participants). Scaling of horizontal and vertical probe offsets is with respect to the midpoint between the two references (illustrated by the large open circles). Negative values: probes more foveal/below, positive values: probes more peripheral/above the midpoint. In this notation, fixation was at -12 deg.

Experiment 1a: Figure 2 illustrates the actual (black dots) compared to theperceived (colored dots) probe positions for each of the 36 tested locations in the three conditions of Experiment 1a, averaged over all eight participants. First,focusing on*mislocalizations along the horizontal axis*, Figure 2A and 2Bshow that in the references-only condition and the mask-only condition, most probes were seenmore foveallythan their actual location. The foveal bias decreased the closer the probes were presented to fixation. This pattern of mislocalizations for briefly flashed peripheral stimuli is consistent with previous reports of foveal bias(Kerzel, 2002; Mateeff & Gourevich, 1983; O'Regan, 1984; Sheth & Shimojo, 2001; van der Heijden, van der Geest, de Leeuw, Krikke, & Müsseler, 1999).However, somewhat unexpectedly, in the two control conditionsthe probes nearest to fixation were seen close to their actual location or even with a small peripheral bias, making responses seem to converge towards the position at -2 deg. In contrast, the pattern of perceived probe locations in the criticalreferences+mask condition (Figure 2C) showed strong bi-directional horizontal compression towards the reference axis: probes presented more peripherally

than the references were pulled in,and probes presented more foveally than the references were pulled outwards. In other words, even if presented with horizontal offsets as big as 3 deg from the imaginary vertical line joining the two references, responses were converging towards 0 deg, that is, probes on both sides were seen almost aligned with the references.

To test for differences in the strength of compression effects across conditions, we first averaged each participant's data for each horizontal probe position, poolingover vertical offsets. Then we plotted the resulting perceived locations against actual horizontal positions and fitted linear regressions to each participant's data in the three conditions. Figure 3A shows actualagainstperceived locations averaged across the eight participantsand the corresponding linear regression lines. Since we used linear regressions, the slope and bias parameters of these fits are identical to the mean slopes and mean biases when averaging over the individual fits.We used the slope of the linear fits as an estimate of compression: If perception was veridical and without compression (i.e., actual = perceived location), the slope should be close to b = 1, if all stimuli were perceived fully compressed towards one single location, a flat line should emerge with a slope close to b = 0. The inset of Figure 3A shows the average slopes for the three conditions based on the individual fits of theeight participants. All slopes are smaller than b = 1, indicating that there was some compression in all conditions. However, a repeated-measures one-way ANOVA revealed a significant main effect, $F(2,14) = 14.85$, $p < .001$, confirming that the slopes were different across conditions.Subsequent pairwise t-tests confirmed a significantly shallower slope, that is, more compression, for the references+mask condition compared to both the references-only conditionand the mask-only condition, $ts(7)>3.70$, $ps< .008$. The difference between the slopes for the references-only and mask-only condition was not significant, $t(7) = 1.63$, $p = .148$.[1]

[1]As an alternative way of testing for horizontal compression, we conducted a 3 (condition) x 6 (probe location) repeated measures ANOVA that revealed an interaction between the two factors, $F(10,70) = 9.22$, $p < .001$, confirming less spread in the mean localization responses across the six locations in the references+mask condition than in the other two conditions. Comparing localization at each probe location separately, pairwise t-tests revealed significant differences between the references+mask and both control conditions only for the two probe locations closest to fixation (-3 deg and -1.5 deg: $ts(7) > 2.76$, $ps< .028$; all other comparisons: $ps> .137$). Nonetheless, a 3 (condition) x 3 (probe location) repeated-measures ANOVA only taking into account the three more peripheral probe locations (+0.5 deg, +1.5 deg, + 3 deg) for which no pairwise differences were found, still produced the critical interaction, $F(4,28) = 8.44$, $p < .001$, indicating less spread (= stronger compression) in the responses across probe locations in the references+mask condition compared to the two control locations at these peripheral probe locations.

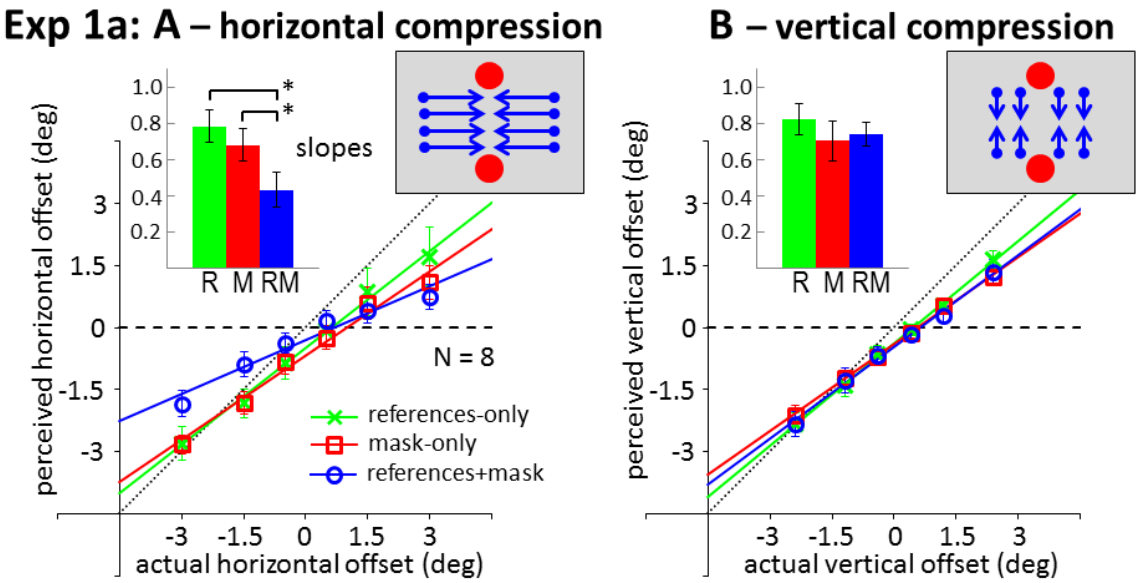

Figure 3. Actual vs. perceived probe locations in Experiment 1a (mouse responses), separate for horizontal (*A*) and vertical offsets (*B*),and the corresponding linear fits. Horizontal black dashed lines illustratea slope of b = 0 (i.e., full compression), black dotted diagonal lines illustrate a slope of b = 1 (i.e., no compression).Error bars at each data point represent the standard error of the mean. The inset bar graphs show the slopes of the regression lines for each condition, averaged across the individual fits forour eight participants. Error bars of the slopesdenote within-subjects 95%-confidence intervals(Bakeman & McArthur, 1996).

To describe*mislocalizations along the vertical axis*, Figure 2shows that in all three conditions, most probes were seen slightly below their actual location and this downward bias seemed stronger the further up the probes were presented. Interestingly, there was no sign of stronger (bi-directional) compression, or of competition between the two references in the references+mask condition. One might have expected, for instance, that probes presented above the midpoint are drawn towards the upper reference and probes presented below the midpoint towards the lower reference dot. Such a pattern would result in slopes of b > 1 when plotting actual against perceived location. Figure 3B shows actual vertical probe positions againstthe averaged perceived locations, pooledover horizontal offsets, and the corresponding linear fits for the three conditions.All slopes were shallower than b = 1. The one-way ANOVA on the slope parameter did not reveal a significant main effect of condition, $F(2,14) = 1.77$, $p = .206$, confirming the vertical compression in the references+mask condition was not stronger than in the other two conditions. These results indicate thatstronger compressioncaused by the mask were restricted to the horizontal axis (Figure 3A), with probes being drawn towards the gap between the two references in the references+mask condition.

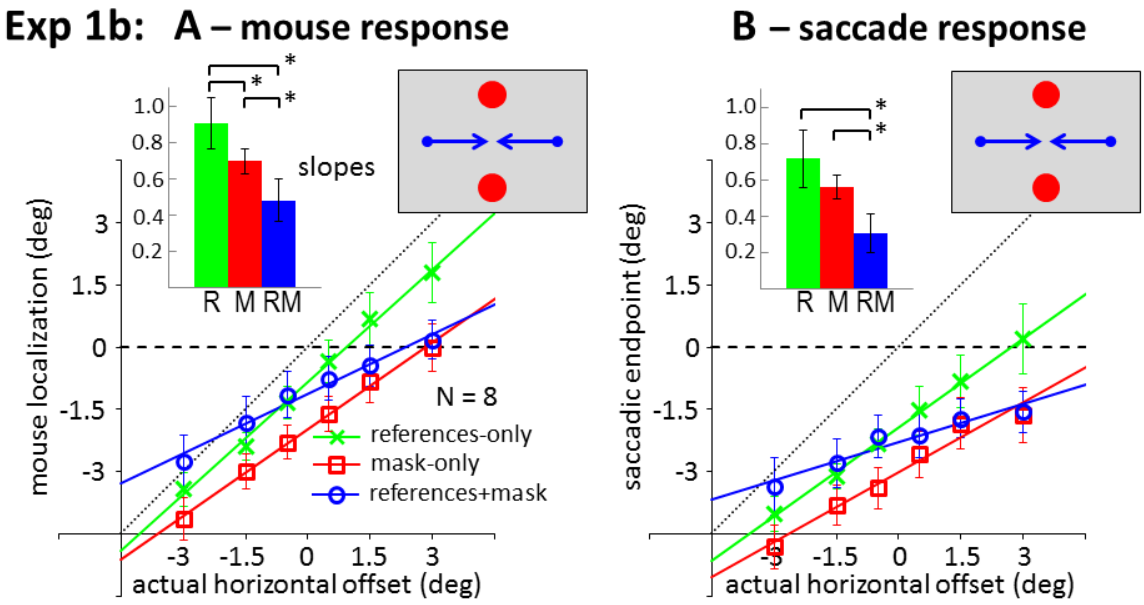

Figure 4.Actual vs. perceived horizontal probe locations in Experiment 1b, separate for mouse responses (*A*) and saccadic responses (i.e., saccadic endpoints, *B*), and the corresponding linear fits.Conventions as in Figure 3.

Experiment 1b: Figure 4A plots actual probe locations against the mouse localization responses (similar to Experiment 1a) and the corresponding linear fits for the six horizontal probe positions used in Experiment 1b (no vertical offsets were presented). Figure 4B plots actual probe locations againstsaccadic localization responses, that is, saccade landing positions.Comparing themouse response graph (Figure 4A) to the results of Experiment 1a (Figure 3A), most lines are shifted downward on the graph, and so closer to fixation (at -12), reflecting a stronger foveal bias. This shift is even larger for the saccade landing positions (Figure 4B). The strong foveal bias in saccade landing positions is not unexpected, as saccades generally undershoot their targets.The explicit eye movement instruction may have made participants more aware of their saccade landing positions, which may in turn have biased the mouse responses more strongly towards the fovea as well.In any case, comparing the slopes, the patterns for both mouse responses and saccade responses are quite similar to the mouse response slopes of Experiment 1a: the shallowest slope, that is the strongest compression, is found for the references+mask condition. For both mouse pointing responses and saccade localization responses, the one-way ANOVAson the individual slope values revealedsignificant main effects of condition,mouse clicks: $F(2,14) = 13.53$, $p = .001$, saccades: $F(2,14) = 11.83$, $p = .001$.For the mouse pointing responses, all subsequent pairwise *t*-tests, including references-only vs. mask-only, were significant, *t*s(7)

>2.70, *ps*< .031. Pairwise t-tests on the saccade data only revealed significant differences between the references+mask condition and the references-only as well as the mask-only condition, t*s*(7) > 3.73, *ps*< .007, but no significant difference between the references-only and the mask-only condition, *t*(7) = 1.71, p = .131. Results from Experiment 1b thus suggest that compression does not depend on the response modality. Localizing the probes by directing saccades towards their perceived location is subject to the same mislocalizations as mouse pointing responses. We want to stress again that the obtained results donot reflect the classic finding of saccadic compression of space. Compression in our Experiment 1b is induced by the references and mask, we only measure it after some delay with the help of saccade landing positions. In the classic perceptual illusion, compression of space is induced by the saccade, when the probe is flashed close in time to the eye movement. Note that in our setup the timing of events (probes visible for 8-25 ms, mask for 50 ms, saccade latency around 270-280 ms) was such that the saccade was made well after the probe was removed from the screen. Also, as already mentioned in the introduction, any compression due to the saccade should be directed towards its target which in our case was the probe, not the references.

3. Experiment 2a and 2b: Horizontally arranged pair of references

The results of the first experiments showed probes drawn in towards the space in between the two vertically separated reference stimuli, as if they acted as one single vertically elongatedattractor bar. We cannot tell from these results if horizontal compression is the prominent effect of reference stimuli in general or if some or all of the compression pattern was caused by the spatial layout of the two references. To address this, we repeat the experiment but with a pair of horizontally separated references presented on the horizontal meridian. If the spatial configuration is contributing to the pattern of compression, we may find that it has been rotated with the references, producing now stronger vertical than horizontal compression.

In Experiment 2a, we test mouse pointing responses to the same matrix of 6 x 6 locations used in Experiment 1a. In Experiment 2b, as in Experiment 1b, we test both mouse pointing and saccade landing responses for only the center array of six locations, but now along the vertical axis.

Methods

Participants

Both experiments were again run on eight participants each (Experiment 2a: four men, four women, including two participants from Experiment 1b, mean age: 30.6 years; Experiment 2b: five women, three men, including the same author and twofurther participants from Experiment 1a, mean age: 30.0 years). All participants reported normal or corrected-to-normal vision.

Apparatus, stimuli, design and procedure

Apparatus, stimuli, design and procedure were identical to Experiment 1 with the exception that the stimulus arrangement was rotated by 90 deg: The references were presented on the horizontal meridian, one at a horizontal distance of 8 deg from fixation, the other at 16 deg from fixation. Thus, the midpoint between the two references was again at 12 deg from fixation. Further, the possible horizontal and vertical offsets for the probe were swapped in Experiment 2a: Probes were presented at a distance of either -2.4, -1.2, -0.4, 0.4, 1.2, or 2.4 deg horizontally from the midpoint between the two references, and -3, -1.5, -0.5, 0.5, 1.5, or 3 deg vertically from the horizontal meridian (see Figure 1C). In Experiment 2b in which participants had to direct eye movements to the probe, the probes were presented without any horizontal offset from the midpoint between the two references, but with the same vertical offsets as used in Experiment 2a.

Results and Discussion

Error trials and probe duration

Experiment 2a: On 2.7% of trials, breaks of fixation or blinks were detected. Participants indicated not to have seen the probe on 1.1% of trials in the references-only condition, 14.8% of trials in the mask-only condition, and 13.3% of trials in the references+mask condition. Average probe duration was 8 ms in the references-onlycondition, and 19 ms in both conditions with the mask. Pairwise t-tests confirmed a significantly shorter duration in the references-only compared to the other two conditions, $ts(7) > 4.87$, $ps = .002$, but no difference between the mask-only condition, and the references+mask condition, $t(7) = 0.20$, $p = .850$.

Experiment 2b: The strict criteria for trial exclusion based on the saccade characteristics led to 13.7% error trials. Participants indicated not to have seen the probe on 0.4% of trials in the references-only condition, 10.6% of trials in the mask-only condition, and 9.1% of trials in the references+mask condition. This resulted in average probe duration of 9 ms in the references-onlycondition, 18 ms in the mask-only, and 19 ms in the references+mask condition. Pairwise t-tests confirmed a significantly shorter duration in the references-only compared to the other two conditions, *t*s(7)>5.78, *p*s< .001, but no difference between the mask-only and the references+mask condition, $t(7) = 1.56$, $p = .162$.

Localization responses

Experiment 2a: Figure 5 illustrates the actual (black dots) compared to the perceived (colored dots) probe positions for each of the 36 tested locations in the three conditions of Experiment 2a. In the references-only and mask-only condition, the pattern looks very similar to the one obtained with vertically arranged references in Experiment 1a: probes were perceived more foveallyand below their actual location.Those mislocalizations seemed to be stronger the further in the periphery and the higher up the probes were presented, accounting for slopes smaller than b = 1 in all conditions (see Figure 6A and 6B).

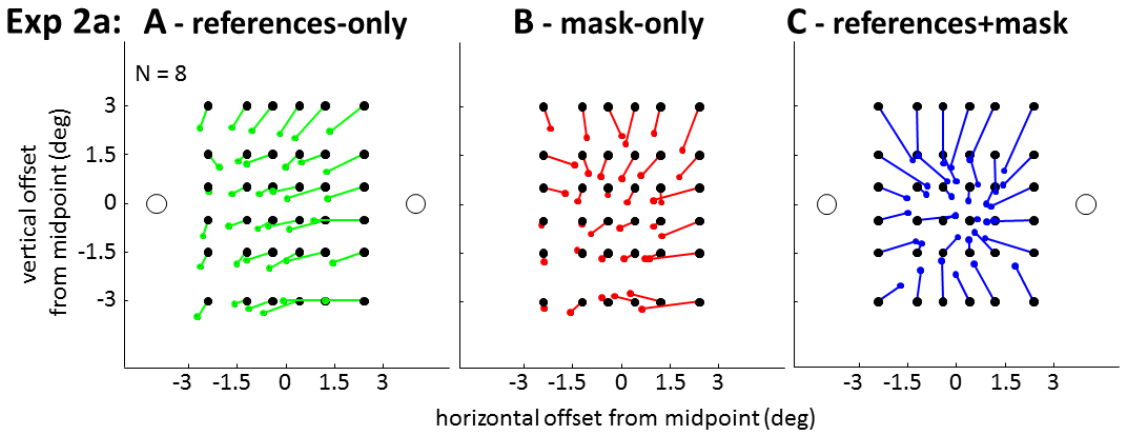

Figure 5. Actual (black dots) vs. perceived (colored dots) probe location for the 36 tested locations in the three conditions of Experiment 2a. Conventions as in Figure 2.

In contrast, the pattern of perceived probe locations in the references+mask condition seems to be characterized bybi-directional compression along the horizontal and vertical axis: probes were seen closer to the midpoint between the references than they were actually presented. Figure6Aillustrates slopes whenplotting actual against perceived location for the six*horizontal probe positions*, pooled across vertical positions. There was only a

marginally significant main effect of condition, $F(2,14) = 3.20$, $p = .072$, confirming a tendency for slightly more compression along the horizontal axis in the references+mask condition.Figure 6B shows actual against averaged perceived locations for each *vertical probe position* across horizontal offsets, and the corresponding linear fit. The one-way ANOVA on the slopes revealed a significant main effect of condition, $F(2,14) = 18.26$, $p < .001$. Subsequent pairwise t-tests confirmed a significantly shallower slope, that is more compression along the vertical axis, for the references+mask condition compared to both, the references-only condition and the mask-only condition, $ts(7) > 3.55$, $p < .009$. The difference between references-only and mask-only condition was not significant, $t(7) = 1.19$, $p = .271$. Thus, similar to Experiment 1, compression in the references+mask condition was stronger orthogonal to the references axis, such that participants were seeing the probes more aligned with the references than they actually were. Comparisons between experiments revealed that references+mask was the only condition that revealed differences in slopes: There was a marginally significant difference for mislocalizations along the x-axis,$t(14) = 1.92$, $p = .076$, indicating a small tendency for more horizontal compression with the vertical reference arrangement; and there was significantly stronger vertical compression with the horizontal arrangement, $t(14) = 2.45$, $p = .027$. The slopes in the references-only and and mask-only conditions did not differ significantly across the two experiments, all $ts < 1.70$, all $ps < .111$.

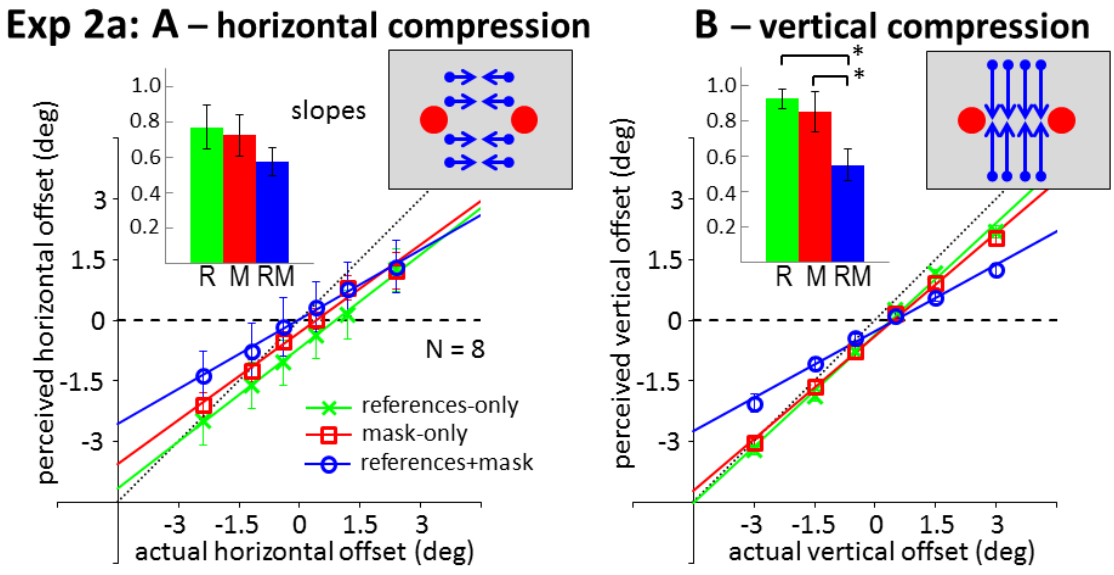

Figure 6. Actual vs. perceived probe locations in Experiment 2a (mouse responses) and the corresponding linear fits, separate for horizontal (*A*) and vertical offsets (*B*). Conventions as in Figure 3.

Although only marginally significant, it is interesting to note that there was some variation in perceived probe locations across the three conditions along the horizontal axis as well. Figure 5, illustrating the mean across our eight participants, seemingly indicates that responses were biased towards the midpoint of the two references. However, Figure 7B, illustrating individual data in the references+mask condition, paints a different picture.There seems to be sometendency for seeing the probe closer to one or the other reference. There ishowever, considerable variation in these patterns across individuals with some participants reporting the probe closer to the more foveal reference (e.g. S1, S4, or S6), whereas others report the probe closer to the more peripheral reference (e.g. S2, S3, or S5).

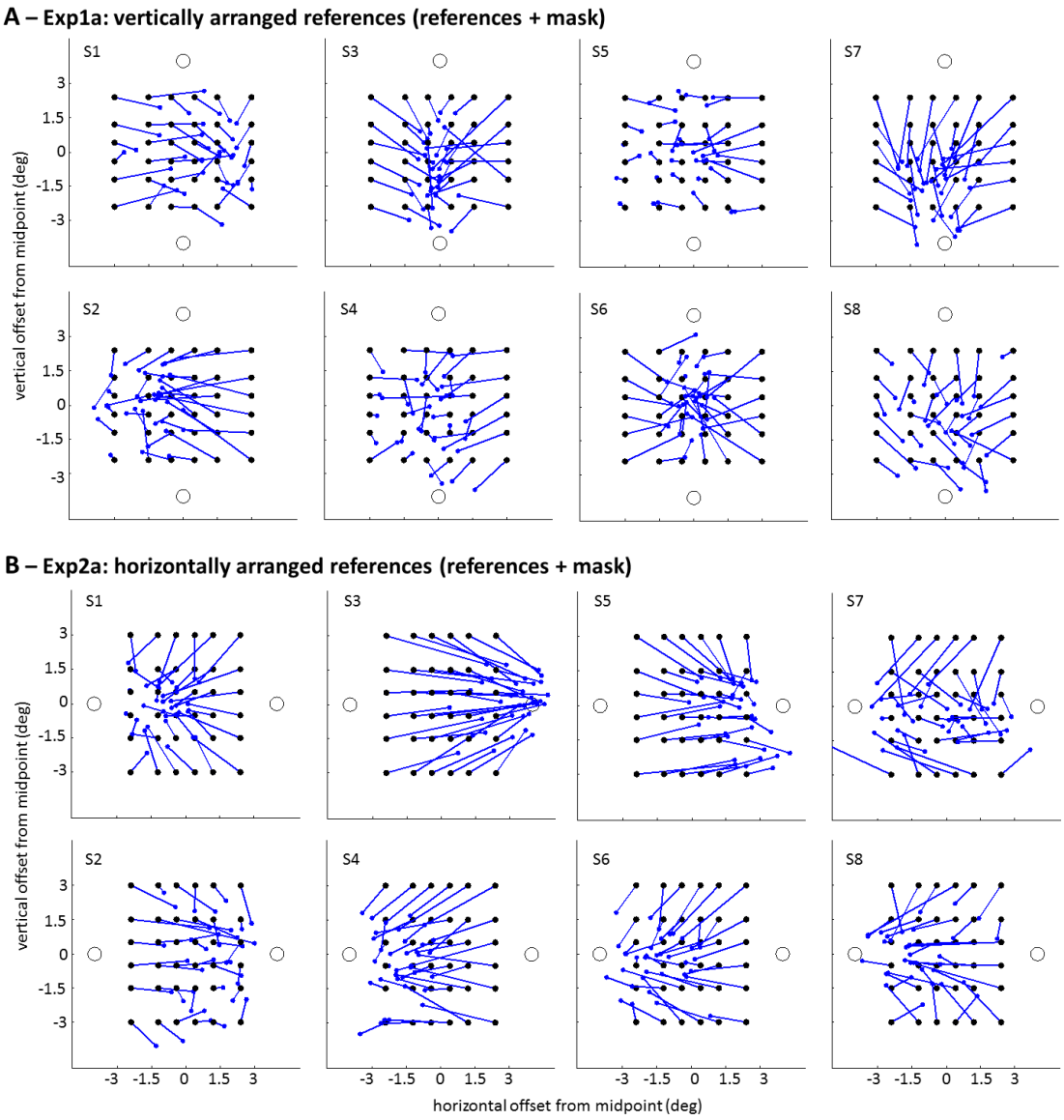

Figure 7. Actual (black dots) vs. perceived (blue dots) probe location for the 36 locations in the references+maskcondition, individuallyfor all eight participants tested in Experiment 1a (*A*) and Experiment 2a (*B*). Conventions as in Figure 2.

To compare, Figure 7A shows that responses with vertically arranged references in Experiment 1a, although again showing some variation, mostly show a general downward bias that was also present in the control conditions. Importantly, they did not show an attraction to one or the other reference. We have no explanation as yet for these differences between the horizontal and vertical references.

Whatever their origins, we want to stress that the idiosyncratic attraction effects along the reference axis, to either the left or right reference in Experiment 2a,do not affect our main conclusions concerning compression orthogonal to the reference axes. First, with only small variations (e.g, S1 or S2 in Experiment 1a), responses converge toward the reference axes (that is, not left or right of it in Experiment 1a; not above or below it in Experiment 2a). Second, attraction to one reference or the other along the reference axis will affectthe intercept of the linear fit along the reference axis (e.g. Fig 6A, Fig. 3B), but does not affect the slopeorthogonal to the reference axis that we use as our orthogonal compression index. Third, the statistical analyses on which we based our conclusions were run on individual participant's parameter fits. The pooling only occurred (within each participant) across vertical probe locations when we looked at horizontal compression and vice versa. As such, our analyses do not capture any interactions that might have occurred between horizontal and vertical compression. But the effects of the idiosyncratic patterns are included in our repeated-measures ANOVAs: the stronger compression (i.e. shallower slopes) in the references+mask condition found along the horizontal axis in Experiments 1a and 1b with vertically arranged references, and along the vertical axis in Experiment 2a (and 2b; see below) with horizontally arranged references, reflect that despite possibleinterindividual differences in compression centers, there is consistently more compression in the references+mask condition than in the other two conditions when comparing the slopes within-subjects.

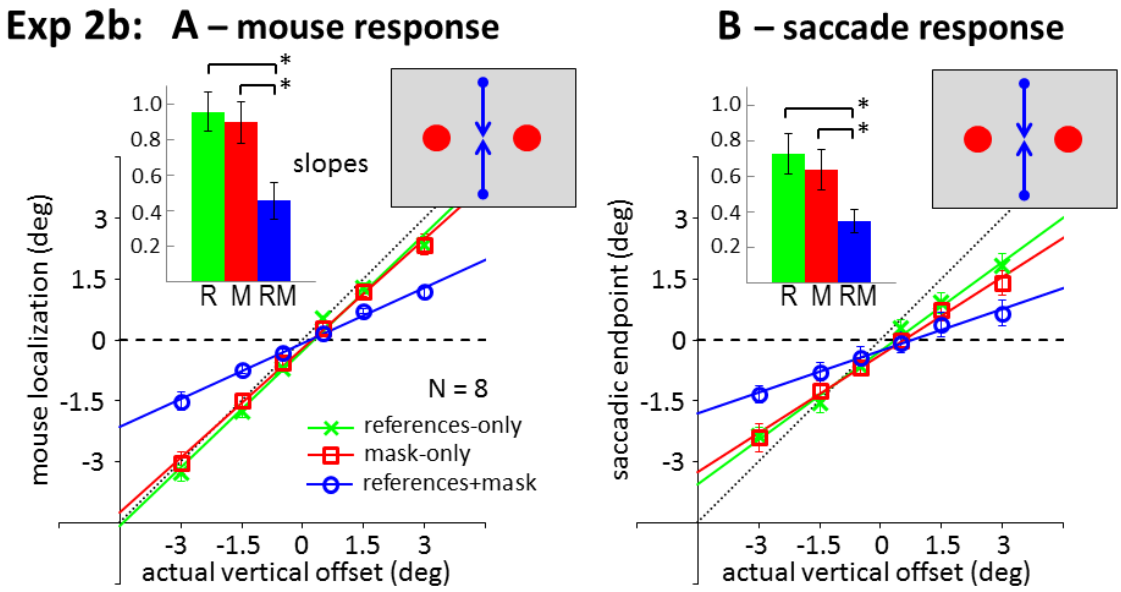

Figure 8.Actual vs. perceived vertical probe locations in Experiment 2b, separate for mouse responses (*A*) and saccadic responses (i.e., saccadic endpoints, *B*), and the corresponding linear fits.Conventions as in Figure 3.

Experiment 2b: Figure 8A plots the mouse pointing responses against actual probe locations and the corresponding linear fits for the six vertical probe positions used in Experiment 2b. Recall that all probes were presented without horizontal offset from the midpoint between the two references. Figure 8B plots saccade landing positions against actual probe locations. Results look very similar to the vertical compression found in Experiment 2a (Figure 6B): the shallowest slope, that is the strongest compression, is found for the references+mask condition for both mouse and saccade responses. In general, the saccade slopes in all three conditions are slightly shallower than for the mouse responses. For the slope parameter, both ANOVAs revealed significant main effects of condition, mouse pointing: $F(2,14) = 22.75$, $p < .001$, saccades: $F(2,14) = 14.90$, $p < .001$. For both measures, the slopes in the references+mask condition were significantly different from the slopes in the mask-only and the references-only condition,mouse pointing: $ts(7) > 5.34$, $ps < .001$, saccades: $ts(7) > 4.71$, $ps < .002$. But there was no significant difference between the references-only and the mask-only condition,mouse pointing: $t(7) = 0.71$, $p = .502$, saccades: $t(7) = 0.98$, $p = .360$.Thus, the pattern in saccade landing positions is very similar to the vertical compression we found with mouse pointing responsesalready in Experiment 2a.

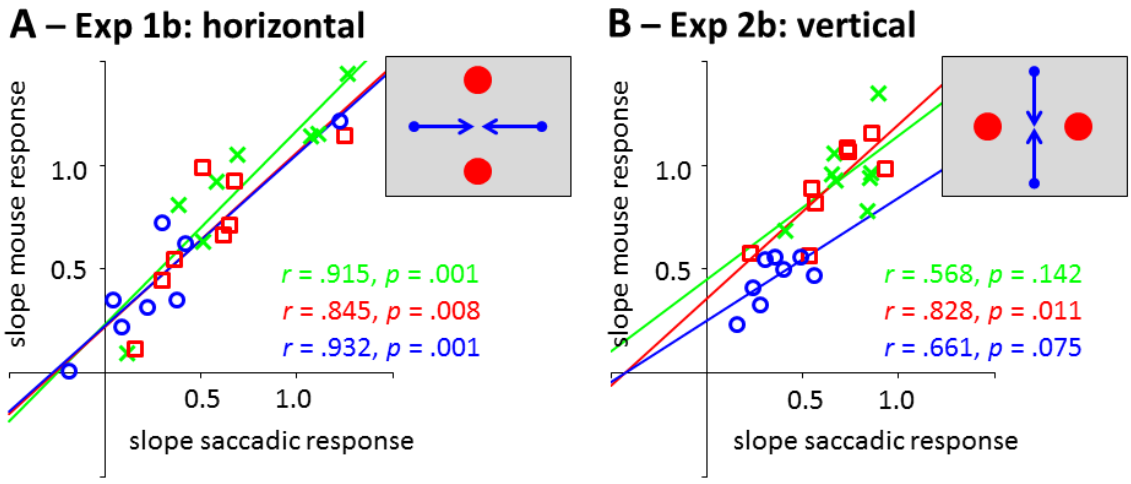

Figure 9.Slopes of the linear fits obtained for saccade responses against slopes obtained for the mouse responses in Experiment 1b (*A*) and Experiment 2b (*B*), and the corresponding bivariate correlation parameters. Green crosses: references-only condition, red squares: mask-only condition, blue circles: references+mask condition.

Finally, to see whether compression in mouse responses covaried with compression in saccade responses, we correlated the slopes obtained for the two response modes across the eight participants for both vertically aligned references (Experiment 1b) and horizontally aligned references (Experiment 2b). Figure 9A shows that for all three conditions, the amount of horizontal compression in saccade responses was strongly correlated with the amount of horizontal compression in the mouse responses across participants. However, for vertical compression, the correlations between the slopes obtained for the two response modes across the eight participants (Figure 9B) are generally weaker. Only the mask-only condition shows a significant correlation.

4. General Discussion

The current experiments were designed toelaborate on the phenomenon of mask-induced compression. In four experiments, we extend our previous findings (Zimmermann, Born, et al., 2014; Zimmermann et al., 2013):Compression-like mislocalizations of briefly flashed probes can be observed with stationary eyes when presenting a visual reference stimulus and masking the probe.The pattern resembles the typical mislocalizations previously reported around the time of saccadic eye movements (Honda, 1993, 1999; Lappe et al., 2000; Morrone et al., 1997; Ross et al., 1997) or of image motion simulating the visual effects of saccades (Ostendorf et al., 2006). Although the current experiments examined

only a rather restricted range of probe eccentricities between -3 deg and +3 deg from the references, our previous experiments have demonstrated larger mislocalizations of probes as far out as 8 deg from the references and 20 deg from fixation. Further, saccade- and mask-induced compression have been found to be of similar magnitude in equivalent paradigms using the same stimuli (Zimmermann, Born, et al., 2014; Zimmermann et al., 2013)). In general, our findingsstrongly suggest that compression of space is not a purely oculomotor phenomenon, critically dependent on saccade-specific phenomena like corollary discharge signals or the updating of eye position signals. In contrast to our previous reports, here we always presented two references, either vertically arranged or horizontally arranged. In both cases, we found clear evidence for bi-directional compression only orthogonal to the reference axis as opposed to along it, flexibly changing with the stimulus arrangement. Further, compression was also found whensaccades were aimed at the probe as a method of reporting their perceived location.

Prerequisites of mask-induced compression

We compared compression in the critical references+mask condition to two controls: a references-only and a mask-only condition. In previous experiments, analogous to saccadic compression experiments, we only varied the timing between the references, the probe and the mask and found compressionif the probe was presented close in time to the mask(Zimmermann, Born, et al., 2014; Zimmermann et al., 2013). The first control condition without mask in the current study confirmed the crucial role of the mask in inducing compression.

Our second control condition demonstrated the importance of visual references in mask-induced compression (see also Zimmermann, Morrone, & Burr, 2014 for saccadic compression). Moreover, presenting the masked probe without the referencesruled out the possibility that the strong bi-directional compression effect in the references+mask condition simply reflects a central tendency of judgment, that is, a bias to click towards the center of the distribution of probe locations(e.g. Hollingworth, 1910; Poulton, 1979; Spencer & Hund, 2002; Stevens & Greenbaum, 1966).In fact, such a bias towards the mean may have played a role in all three conditions and, combined with a foveal bias, may explain why responses also converged in the two control conditions, towards - 2 deg from the references axis. One may expect such a strategic bias especially under conditions of low visibility, on

trials when the probe was barely seen. In our experiments,however, despite lower visibility (see results of the staircase procedure), the pattern of mislocalizations in the mask-only control was very similar to the references-only control. On the other hand, despite similar visibility of the probe in the mask-only control and the critical references+mask condition, strong bi-directional compression towards the reference axis was only found when both references and mask were present. Furthermore, biases towards the mean of the probe distribution cannot explain why the dominant compression axis in the reference+mask condition was dependent on the arrangement of the references, while the unidirectional compression tendencies in the two control conditions were not. Thus, in line with previous research on saccadic compression(e.g. Honda, 1999; Lappe et al., 2000), the mask-induced compression found in our references+mask condition is not simply a strategic biastowards the mean of the distribution when stimuli are barely seen.

Nonetheless, the visibility of the probe plays a role.For saccade-induced mislocalizations, it has already been demonstrated that effects are weaker with higher probe contrast orluminance(Georg, Hamker, & Lappe, 2008; Michels & Lappe, 2004).We have seen a similar relation in pilot experiments for mask-induced compression.Therefore, we useda staircase procedure in our experiments to adjust probe visibility individually for each participant, in our case by adjusting its duration.Aninspection of the precision in each condition (i.e., the random error or variance in responses at each probe locations; see supplementary Figure SF1) indicated that the mask (mask-only condition) reduced precision compared to the references-only condition. It seems as if this apparent increase in location uncertainty introduced by the mask is partly counteracted in the references+mask condition, albeit at the cost of a systematic error: the compression bias towards the references. Note, however, that our probe was by no means a typical threshold stimulus, invisible on a large proportion of trials. The staircase procedure followed a four-down, 1-up rule, targeting the 84%-detection threshold and indeed, participants reportedthat they had not seen the stimulus (by clicking on fixation) on only 12%-15% of trials. Further, we made sure that participants did not confuse one of the references with the probe by using different colors.The pattern of mislocalizations in Experiment 1a further demonstrates that the references were not mistaken for the probe: Observers most of times localized the probe in the gap between the two references. Finally, in informal reports, participants repeatedly affirmed to have seen the probe where they had clicked. Thus, although probe visibility modulates compression and location uncertainty might play a role,mask-induced compression is not a phenomenon that requires probes close to detection threshold. In fact, for saccade-induced compression,

participants report to see the probes biased towards the saccade target even if a continuous location marker informs them where the flash is actually presented (Hamker, Zirnsak, & Lappe, 2008).

Flexibility of compression anddirectional biases

For both vertically and horizontally arranged references, we found bi-directional compression only orthogonal to the reference axis. Thus, the direction of compression changed flexibly with stimulus arrangement, underlining the strong dependence of compression on the configuration of the references.Previously we have demonstrated the flexibility of compression by showing that its strength depends on the similarity between the references (or the saccade target) and the probe for both mask-induced and saccade-induced compression (Zimmermann, Born, et al., 2014): using bars, compression is stronger when the probe bar has the same orientation as the reference bar. Others have shown that horizontal mislocalizations of briefly flashed probes may not necessarily be centered on the immediate saccade target. Cicchini and colleagues (Cicchini, Binda, Burr, & Morrone, 2013)demonstrated that when the probe and an additionally presented post-saccadic reference bar had the same orientation, the center of compressionwas horizontally shifted towards thereference bar, away from the saccade target.Moreover, Lavergne and colleagues (Lavergne, Dore-Mazars, Lappe, Lemoine, & Vergilino-Perez, 2012)showed that localizing probes flashed during a first saccadeis influenced by the requirement to make a second saccade. Interestingly, probes presented spatially in between the two saccade targets were mislocalized towards the second, more peripheral saccade target.

The current experiments showthat at least for mask-induced compression, the arrangement of visual references does not only influence the strength or center of compression on a given axis. It also determines the angular direction ofthe prominent compression axis (from horizontal to vertical).The finding that mask-induced compression is strong along one axis and absent orthogonal to this axis is reminiscent of an asymmetry found during saccades. Over large parts of the central visual field, saccadic compression occurs predominantlyparallel to the saccade vector; strong compression orthogonal to the saccade vector has only been reported in one experimental series for probes presented at eccentricities of more than 20 deg from fixation (Kaiser & Lappe, 2004). In saccadic compression, variations of compression with position have been explained by a relationship with cortical magnification(Hamker, Zirnsak, Calow, et al., 2008; Richard et al., 2009;

VanRullen, 2004). Our asymmetry is more difficult to explain and it remains unclear whether the two are related. It is interesting, however, that saccadic compression orthogonal to the saccade was found when using point-like probes (Kaiser & Lappe, 2004), instead of bars elongated parallel to the saccade vector(Morrone et al., 1997). Thus, the asymmetry found in saccadic compression may also be strongly stimulus-dependent(Kaiser & Lappe, 2004), like our mask-induced compression.

Robustness of mask-induced compression: no dissociation between perception and rapid probe-directed actions

In Experiment 1b and Experiment 2b, we have seen that saccades directed towards the probe follow the perceptual illusion of compression: their endpoints are also biased towards the references. Investigating saccadic responses was motivated by earlier findings suggesting that the saccade system and the perceptual system may yield different outcomes for the localization of briefly flashed stimuli (Eggert, Sailer, Ditterich, & Straube, 2002; Hallett & Lightstone, 1976a, 1976b; Wong & Mack, 1981). Also, in a saccadic compression study (Burr, Morrone, & Ross, 2001), blind reaching movements (i.e., reaching with eyes closed or with hands made invisible by a shutter) were not subject to compression, suggesting that compression may not be found with all response modes, and in particular not with open-loop or ballistic responses.

The results of the current experiments, however,rather fit with research reporting no dissociations between saccades and perceptionof briefly flashed targets (Bockisch & Miller, 1999; Dassonville et al., 1992; Lappe, Michels, & Awater, 2010; Zivotofsky, White, Das, & Leigh, 1998). Müsseler and colleagues (Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999; Stork, Müsseler, & van der Heijden, 2010) propose that the foveal bias in the perception of peripherally flashed stimuli may have the same origin as the undershoot typically reported in saccade metrics, supporting a strong coupling between saccades and perception. One decisive factor for dissociations of saccade responses from perception may be the rapidness of saccade execution. De'Sperati and Baud-Bovy(2008)have reported that a motion distractor, known to induce perceptual mislocalizations, biases the endpoints of saccades directed to a briefly flashed target only for eye movements with latencies larger than 250 ms. Saccades made within 100-250 ms of flash onset were directed accurately, suggesting that the influence of the perceptual illusion on saccade landing occurs late. However, Zimmermann and colleagues (Zimmermann, Morrone, & Burr, 2012)have found

strong mislocalizations in a similar task already at saccade latencies of 160 ms. In the current setup, we simply take the similarity between localization responses by mouse clicks and saccades as an indication of the robustness of mask-induced compression.

Possible mechanisms of compression

As already noted above, in the vertical reference arrangement (Experiment 1), participants seethe probes drawn into the space between the two references. Mislocalizations biased towards empty locations in space have already been reported in saccade studies when using antisaccade or saccadic adaptation paradigms (Awater&Lappe, 2004; Awater Burr, Lappe, Morrone& Goldberg, 2005). In those studies, perceived probe locations were biased towards the visually empty location targeted by an antisaccade or the adapted landing position of a saccade, even on catch trials without postsaccadic visual feedback. Our mask-induced compression effects bias the perceived probe locations towards the space in between the two references, such that the three stimuli look more aligned than they were. The effect is reminiscent of higher-level, Gestalt-like principles like the principle of good continuity. Mislocalization biases towards empty locations assumed to be driven by higher-level interpretations of the visual display have also been reported in the memory literature. For instance, the remembered location of a target stimulus may be biased towards the display midpoint (Schmidt, Werner, & Diedrichsen, 2003), the center of prototypical geometric regions (e.g. circle quadrants; Huttenlocher, Hedges, & Duncan, 1991), the imaginary intersection of line elements (Bryant & Subbiah, 1994), or towards the imaginary diagonal when the target is presented in a figure that participants interpret as a graph (Tversky & Schiano, 1989). However, all these biases towards imaginary landmarks as well as biases reported towards or away from actually visible landmarks (e.g. Hubbard & Ruppel, 2000; Kerzel, 2002; Schmidt et al., 2003; Sheth & Shimojo, 2001) are much smaller (minutes of arc or millimeters) than the biases we observed in our references+mask condition or our previous mask-induced compression studies (degrees of visual angle, translating to several centimeters). Therefore we think it unlikely that these effects are strongly related to our mask-induced compression effects. Even more intriguing is the contrast between our results and the attention repulsion effect (Suzuki & Cavanagh, 1997), a bias away from a previously presented flashed attentional cue in a Vernier alignment task, attributed to attention-related receptive field changes. Although small (likewise several minutes of arc), the attention repulsion effect is opposite to what we find in mask-induced compression despite

a quite similar stimulus sequence. Current research in our lab is looking to disentangle the two effects.

Given that we presented a response grid at the end of each trial, one also needs to consider that participants might not have clicked on empty spaceafter all[2].They might have clicked on the grid lines or intersections. As such,our effectscould have less to do with higher-level principles such as spatio-temporal grouping and attraction, but more with the presence ofpostsaccadicvisual references.Specifically, location responses might have been made on the nearest grid line as the only available spatial anchor. However, little evidence for this discretization of responses is seen in the individual clicks and if there were migration to the nearest lines, there are many of them and this would not create the compression effects that we observed. Supplementary Figures SF2to SF5 show the individual clicks of each participants with respect to the references, actual probe locations (both no longer visible during response) and the grid lines. In Experiment 1a, except for subject S3 in the references+mask condition, few clicks were made directly on the vertical grid line joining the two references. In Experiment 2a, clicks on the line marking the horizontal meridian on which the references were placed occurred more often, but not exclusively in the references+mask condition. As mentioned in the introduction, the rationale behind presenting the grid was that previous studies on saccadic compression have demonstrated larger compression effects when a ruler provided a visual reference after the saccade, that is, at the time the localization response was given (Lappe et al., 2000). Thus, a potential influence of the reference grid in mask-induced compression may not be surprising, but may be seen as further converging evidence that similar mechanisms are at play as in saccadic compression. We did not compare our results with mouse clicks with and without the grid so its influence remains somewhat speculative in these conditions. However, in Experiments 1b and 2b the response was given by saccading to the remembered probe location.The reference grid was present when the saccade landed but the saccade was probably prepared in large part before it was presented. Still we found a similar pattern of results as in Experiments 1a and 2a.

One mechanism commonly at play in the saccade and masking paradigms that might be critical for compression effects to emerge is covert attention. Some models of peri-saccadic perception already attribute a vital role to attention(Hamker, Zirnsak, Calow, et al., 2008; Ziesche & Hamker, 2011, 2014). Oculomotor and attentional neural circuits widely overlap

[2] We thank two anonymous reviewers for pointing this out to us.

and oculomotor structures areassumed to be involved in guiding the allocation of spatial attention(Corbetta et al., 1998; Fecteau & Munoz, 2006; Hamker, 2004; Itti & Koch, 2000; Schall, 2004). Thus, a shift of visuo-spatial attention may be the common mechanism behind saccadic and mask-induced compression. Indeed, the abruptly appearing references in our setup were likely to have drawn covert spatial attention towards them. Our previous observation of weaker masked-induced compression with probes following the references by more than 200 ms is also consistentwith attentional contributions (Zimmermann et al., 2013): It has been established that the impact of reflexive attention shifts is similarly brief, declining after 150 - 200 ms (Nakayama & Mackeben, 1989). In this context, one might be tempted to assume that our masked-induced compression effects were after all saccade-specific: the references might have provoked the preparation of a reflexive saccade program towards them, encoded on a common priority map for saccades and spatial attention (e.g. Fecteau & Munoz, 2006; Itti & Koch, 2000). In accordance with instructions, participants were simply withholding this prepared movement. This may well be the case, but as such an explanation refers to structures assumed to commonly guide eye movements as well as *covert* attention, the effects are by definition not exclusively oculomotor in origin.

One attentional component that might be seen as saccade-specific is the widely demonstrated obligatory pre-saccadic shift of spatial attention towards the saccade target, occurring just prior to the eye movement and strictly time-locked to the saccade (e.g. Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995). However, two recent saccade countermanding studies have demonstrated that initially prepared, but successfully cancelled saccades neither entail attention shifts towards the originally designated saccade target(Born, Mottet, & Kerzel, 2014), nor mislocalizations of flashed stimuli (Atsma, Maij, Corneil, & Medendorp, 2014). Admittedly, successfully cancelling a saccade in preparation might be different from preparing and withholding a saccade until a little later, as was the case in the current experiments where participants were free to look toward the stimuli's location in the later response phase. However, the probe was presented too early to fall into the temporal range of these saccades'attention shifts (i.e., probe more than 250 ms before the saccade). In any case, saccades were made in all three conditions,and therefore they cannot explain why bi-directional compression was only found in the references+mask condition.A more general mechanism must be at play that is not strictly time-locked to saccades and not exclusively operative when eye movements are actually executed. On the other hand, a reflexive shift of covert attention driven by the abrupt onset of the references cannot explain the full pattern of the current results either. The references-only condition

should likewise have provokedthis attentional shift, but mislocalizations in that condition were very similar to the mask-only condition with no references. Thus, it seems compression also depends on a disruption of vision, e.g. through a mask or a saccade around the time of probe presentation.

Which other mechanisms may account for both saccade- and mask-induced compression? The importance of visual factors for saccadic compression has been stressed by Lappe and colleagues (Awater & Lappe, 2006; Lappe et al., 2000; Lappe et al., 2010; Michels & Lappe, 2004). In their two-step theory of peri-saccadic localization (Awater & Lappe, 2006; Lappe et al., 2010), they attribute a critical role to the pre-saccadic encoding of the distance between saccade target and flashed probe. They even demonstrated some compression in fixation conditions with two flashed stimuli and no mask. Their compression effect resulted from mislocalizations of the first stimulus towards the subsequently presented probe. They argue that this was probably due to their probe bar being larger and more intense than the first stimulus, a small flashed dot. In contrast, we demonstrate compression of the flashed probe towards the previously presented references. Further, strong bidirectional compression was dependent on the presence of our mask. We have recently proposed a common framework for saccade- and mask-induced compression (Zimmermann, Born, et al., 2014). In accordance with Awater&Lappe(2006), we think the perceived distance between references and probe plays a critical role. More specifically, we see compression as the signature of a correspondence mechanism that maintains object identities across visual discontinuities such as saccades, blinks or masks (Ullman, 1979). This idea is strongly motivated by the finding that compression is dependent on the similarity between visual references and the probe (Cicchini et al., 2013; Zimmermann, Born, et al., 2014). We suggest that apparent motion signals (Anstis, 1980; Braddick, 1980)contribute to estimating the distance between successively appearing, visually similar stimuli: If there is little or no motion signal, the stimuli must be close together. We suggest that the visual disruption caused by saccades or masks acts to reduce the motion signal between the references (or the saccade target) and the probe. Given a weak motion signal, the probe is interpreted as having appeared much closer to the references than it really was. Not all of ourfindings here are easily incorporated in this tentative framework. For instance, it is not clear, why the asymmetries in the mislocalization responses occur (i.e., horizontal compression with vertically aligned references, vertical compression with horizontally aligned references). Interestingly, attention has been strongly linked to apparent motion (Cavanagh, 1992; Dick, Ullman, &

Sagi, 1987; Verstraten, Cavanagh, & Labianca, 2000; Wertheimer, 1912) and so some combination of attention and correspondence mechanisms may be involved.

Conclusions

In four experiments, we have examined prerequisites, flexibility and robustness of mask-induced compression. We have ascertained that mask-induced compression critically depends on the combination of the mask with the presence of visual references. Further, visibility of the probe plays a role. We have seen that the prominent compression axis changes flexibly, depending on stimulus arrangement. Although it may not be exactly clear from our experiments how saccade- or mask-induced compression will behave in new stimulus arrangements, we can say that compression does not seem to be rigidly directed towards, for instance, the saccade target, the closest reference from the actual probe location(see also Cicchini et al., 2013) or the more foveal reference(see also Lavergne et al., 2012). We have further shown that mask-induced compression is a robust phenomenon: we find it in perceptual judgments as well as saccade localization responses. We have suggested a common framework for saccade- and mask-induced compression based on mechanisms that bridgeacross visual discontinuities. Last, we want to stress that we have not ruled out a role for oculomotor structures or mechanisms in compression. After all there is a large overlap in the structures assumed to control eye movements and, for instance, attention. Instead, we show with these examples of mask-induced compression that the mechanisms underlying compression phenomena cannot be solely oculomotor. Mostcurrent accounts of saccadic compression assume saccade-specific signals like corollary discharge or eye position signals to play a vital role even though many also incorporate mechanisms not exclusive to the eye movement system (e.g. visual factors, attention, cortical magnification). Our results suggest that the saccade-specific signals might not be necessary or, at the least, their role in compression might be overestimated.

Finally, although more general mechanisms have been considered, to our knowledge our studies are the first to actually describe systematic bi-directionalcompression of space similar to saccadic compression in a situation that does not require compensations for large retinal image shifts; that is, situations without an eye movement or image motion simulating the visual effects of saccades.

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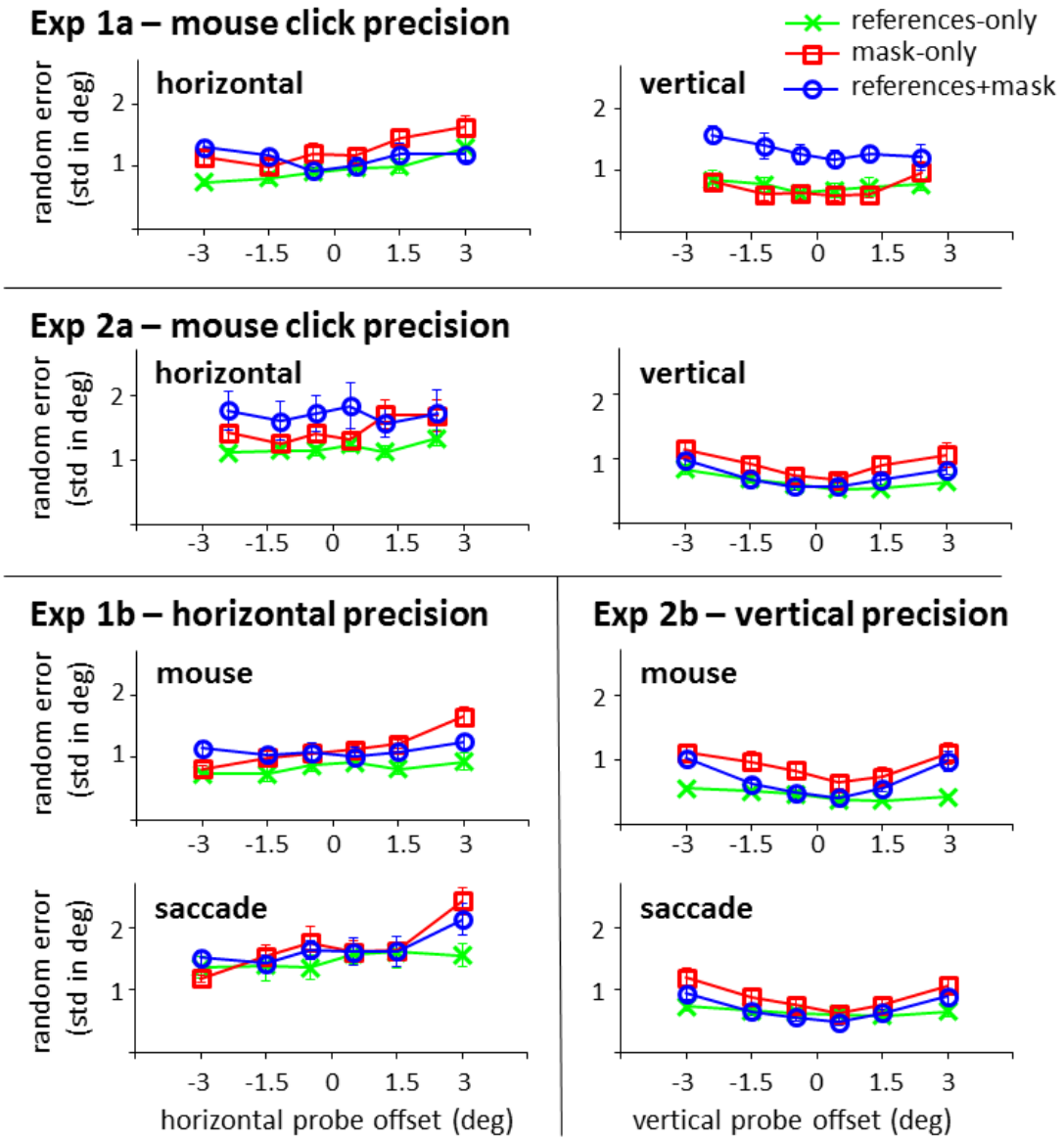
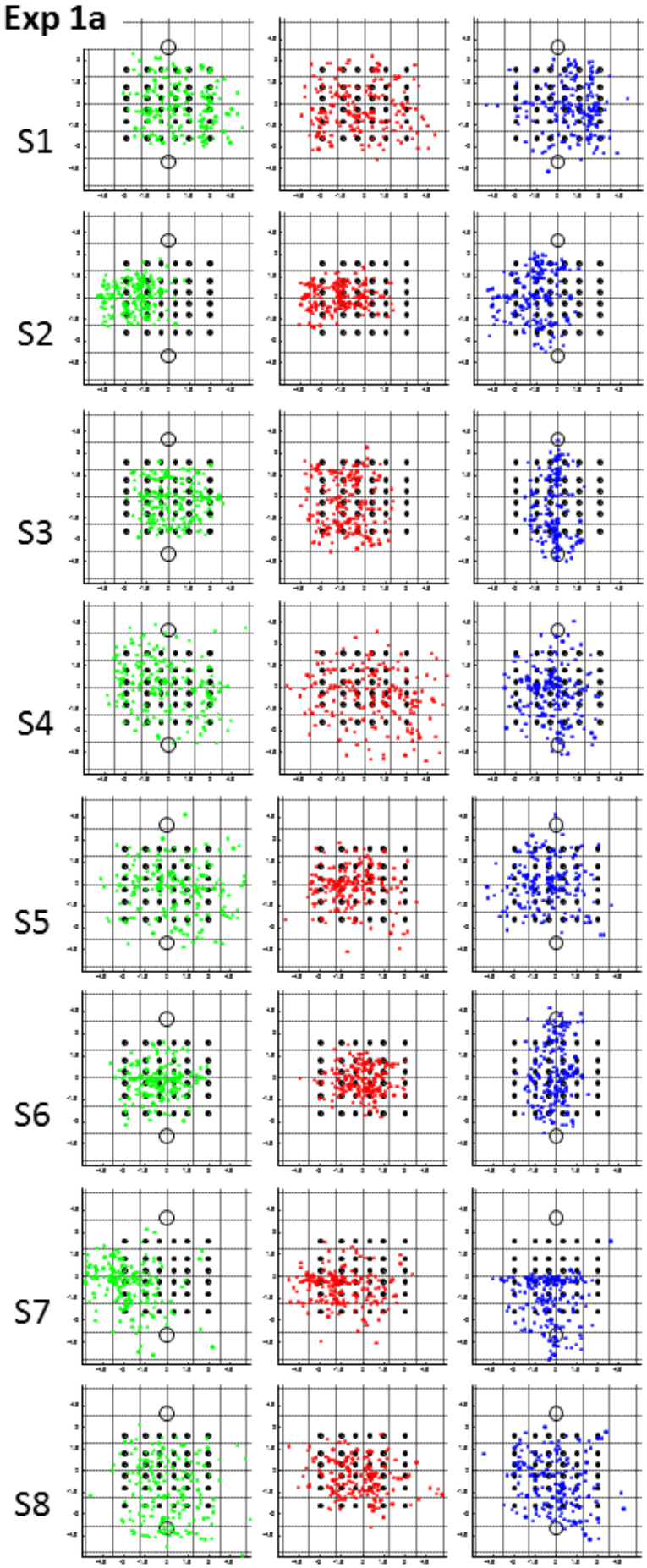
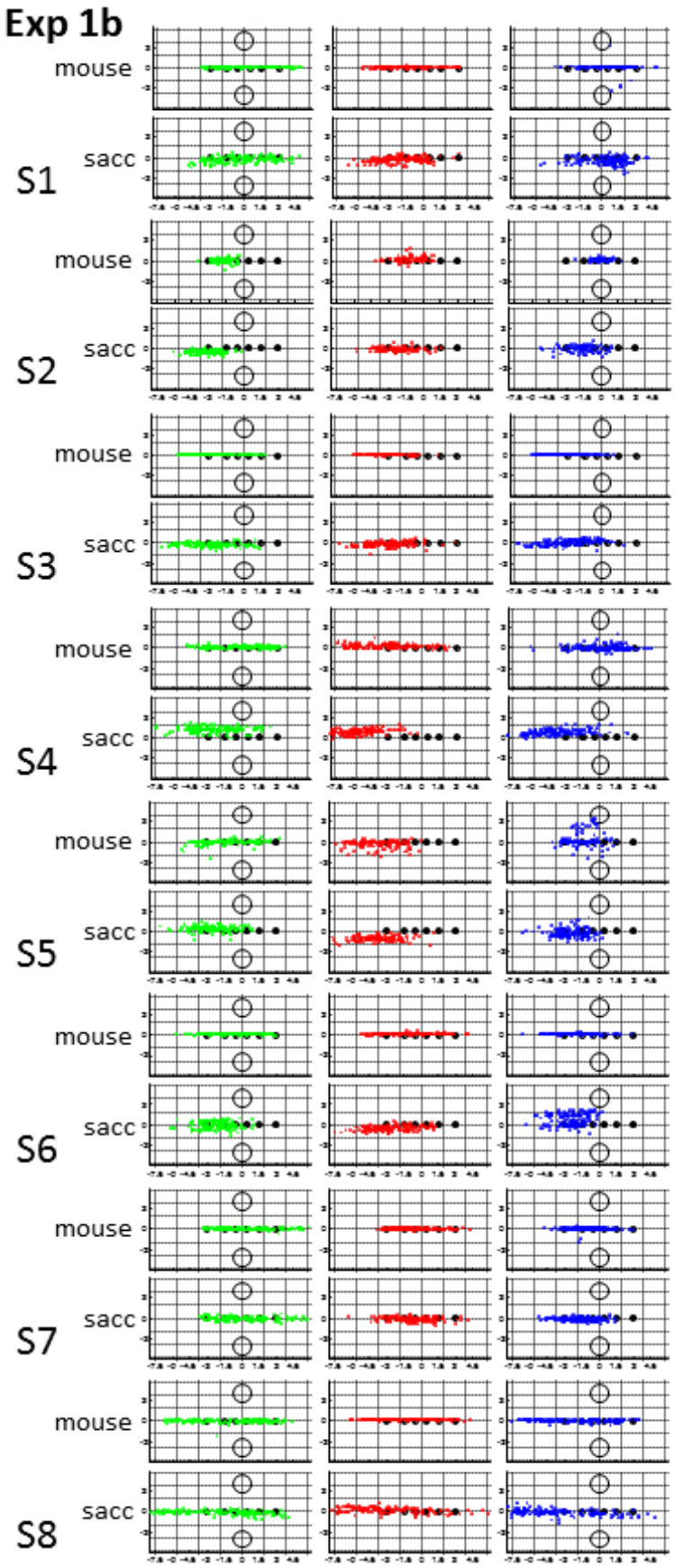


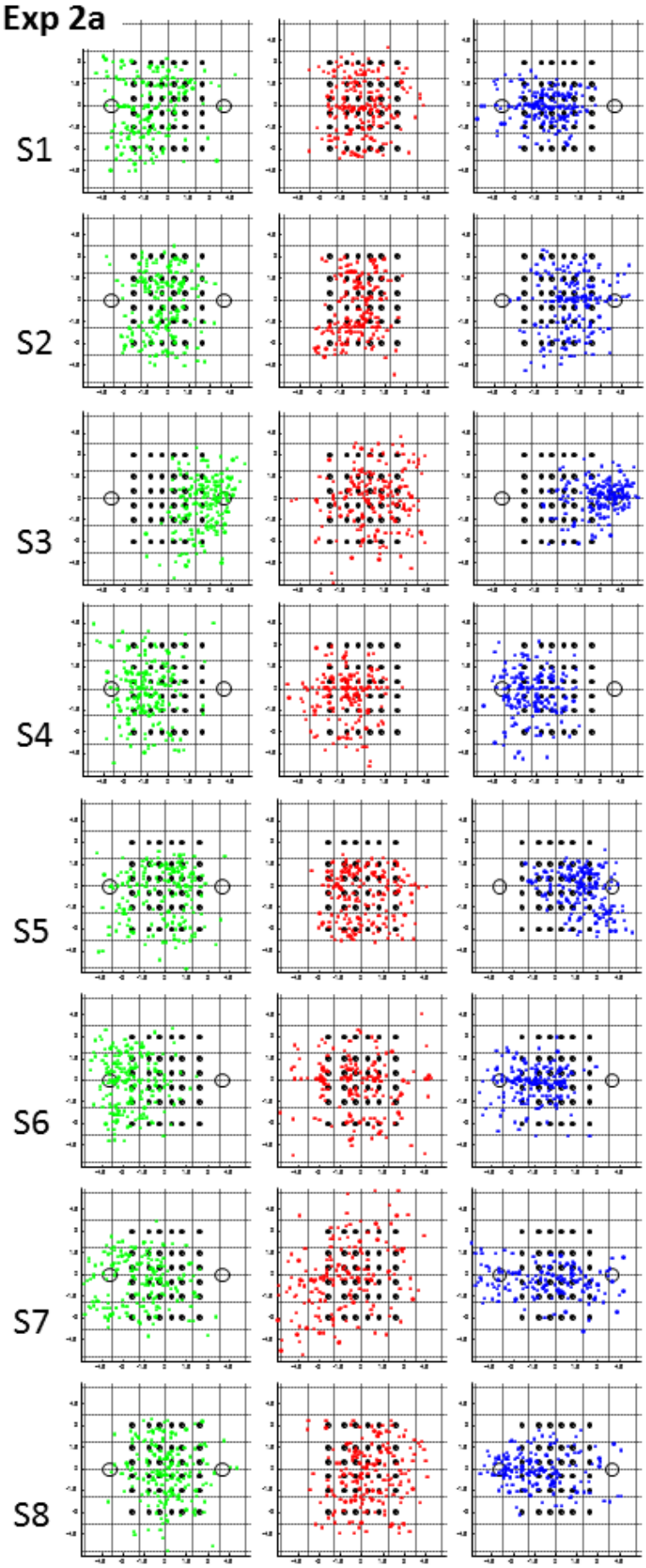
Supplementary Figure SF1.Response precision in the different experiments. Depicted are standard deviations (std) of localization responses, first calculated for every participant, probe location and condition separately, then averaged over participants (error bars represent the standard error of the mean). Thedata represent the random error at each probe location, irrespective of systematic biases in the mean (e.g., compression or foveal bias). For brevity, we will only discuss these data descriptively. In general, there is more random error, i.e., less precision in the mask-only condition compared to the references-only condition (red vs. green).We interpret this as an increase in location uncertainty through the mask. In conditions in which we found evidence for compression (i.e., along the horizontal axis in Exp 1a and 1b, along the vertical axis in Exp 2a and 2b) the random error in the references+maskcondition (blue) most of times lies in between the two control conditions. Thus, precision is somewhat increased compared to the mask-only condition, albeit at the cost of a systematic bias (i.e., the compression bias we describe in the manuscript). Interestingly, random errors increased orthogonal to the prominent compression axis.That is, vertical random error when horizontal compression was found (Exp1a), and horizontal random error, when vertical compression was found (Exp2a).



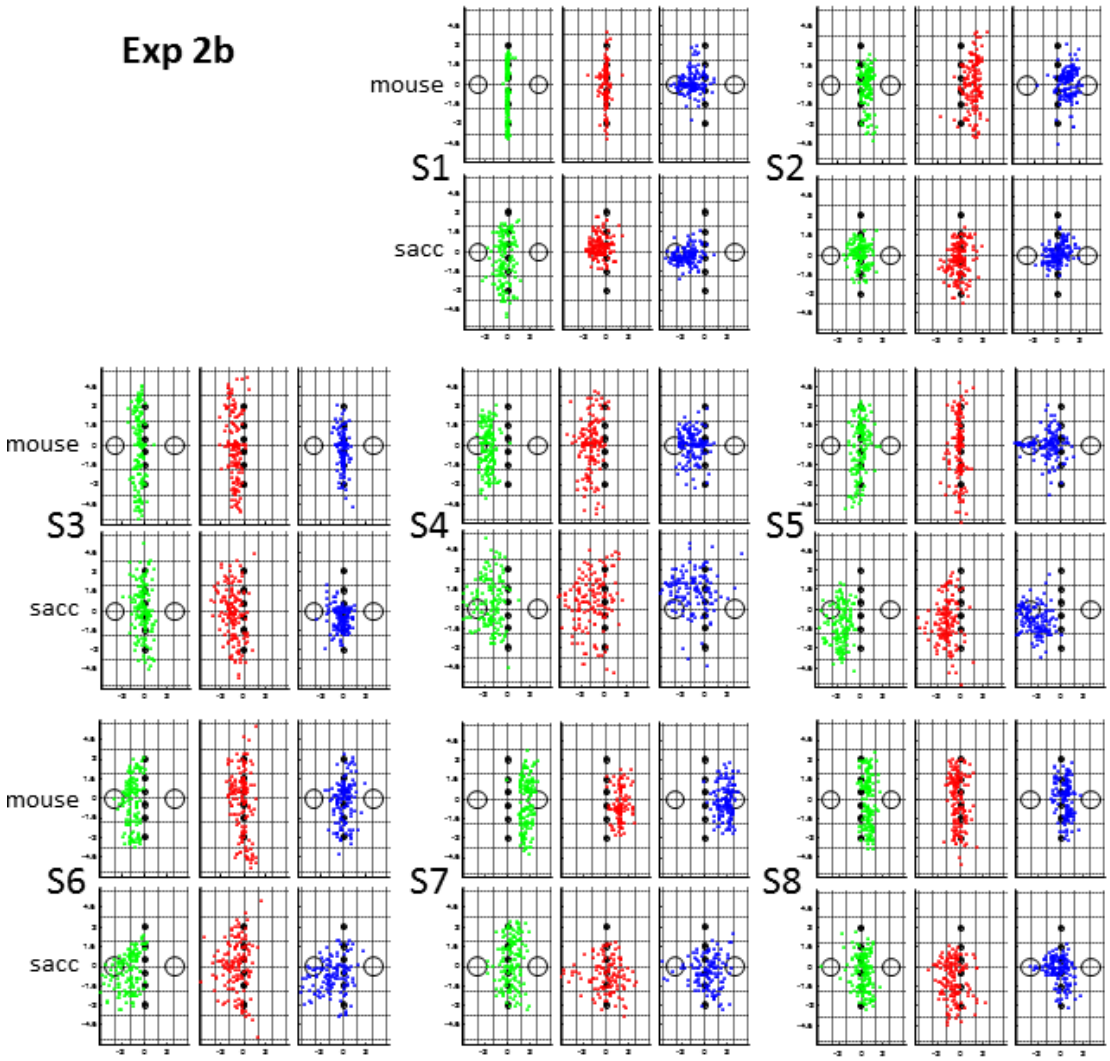
Supplementary Figure SF2. Individual clicks from each trial for all participants (S1–S8) in Experiment 1a in each of the three conditions (references-only: left column, green dots; mask-only: middle column, red dots; references+mask: right column, blue dots) with respect to the references (open large circles, not visible during response), the actual probe locations (black dots, not visible during response) and the response grid lines (visible during response). With exception of subject S3 (references+mask condition), participants rarely clicked directly on the grid line joining the two references.



Supplementary Figure SF3. Individual clicks (mouse) and saccade endpoints (sacc) from each trial for all participants (S1 – S8) in Experiment 1b in each of the three conditions. Only mislocalizations across the horizontal axis were tested, therefore the x-axis is enlarged compared to the y-axis. Otherwise, conventions as in supplementary Figure SF2. No bias to click or land the saccade on the vertical grid lines, in particular the vertical line joining the references (thus fostering compression), is obvious.



Supplementary Figure SF4. Individual clicks from each trial for all participants (S1–S8) in Experiment 2a in each of the three conditions. Conventions as in supplementary Figure SF2. Here, some participants indeed clicked several times on the grid line joining the two references (horizontal meridian), but not only in the references+mask condition, but also in the mask-only condition (see e.g., subjects S1, S4).



Supplementary Figure SF5. Individual clicks (mouse) and saccade endpoints (sacc) from each trial for all participants (S1 – S8) in Experiment 2b in each of the three conditions. Only mislocalizations across the vertical axis were tested, therefore the y-axis is enlarged compared to the x-axis. Otherwise, conventions as in supplementary Figure SF2. No bias to click or land on the horizontal grid lines, in particular the horizontal meridian (thus fostering compression), is obvious in any condition.